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The arbuscular mycorrhizal symbiosis links N mineralization to plant demand

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Abstract Arbuscular mycorrhizal (AM) fungi facilitate inorganic N (NH_4^+ or NO_3^-) uptake by plants, but their role in N mobilization from organic sources is unclear. We hypothesized that arbuscular mycorrhizae enhance the ability of a plant to use organic residues (ORs) as a source of N. This was tested under controlled glasshouse conditions by burying a patch of OR in soil separated by 20-μm nylon mesh so that only fungal hyphae can pass through it. The fate of the N contained in the OR patch, as influenced by *Glomus claroideum*, *Glomus clarum*, or *Glomus intraradices* over 24 weeks, was determined using ^{15}N as a tracer. AM fungal species enhanced N mineralization from OR to different levels. N recovery and translocation to Russian wild rye by hyphae reached 25% of mineralized N in *G. clarum*, which was most effective despite its smaller extraradical development in soil. Mobilization of N by *G. clarum* relieved plant N deficiency and enhanced plant growth. We show that AM hyphae modify soil functioning by linking plant growth to N mineralization from OR. AM species enhance N mineralization differentially leading to species-specific changes in the quality of the soil environment (soil C-to-N ratio) and structure of the soil microbial community.

Keywords Arbuscular mycorrhizal fungi · Organic residue decomposition · N mineralization · N mobilization · Soil microbial community composition

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Introduction

Nitrogen (N) availability often limits plant growth. A large amount of N is stored in soil organic matter, but plants generally absorb N as NH_4^+ and NO_3^-, the inorganic forms of N in soil, relying on microorganisms to mineralize N from organic forms. Some plants have developed the ability to directly utilize some simple soluble organic N compounds from soil (Jones and Darrah 1992; Chapin et al. 1993), while others rely on specialized symbiotic associations to exploit organic N sources (Read 1991). While the metabolism of ectomycorrhizal and ericoid mycorrhizal fungi gives their host plant (Abuzinadah and Read 1989; Leake and Read 1990) the ability to use organic matter as a source of N in heath lands and forests, the role of arbuscular mycorrhizae in plant acquisition of organic N is unclear.

The AM fungi are known as obligate biotrophs relying on C provided by their host plant rather than on dead organic matter (Nakano et al. 1999; Sawers et al. 2008). Most of the literature related to the role of arbuscular mycorrhiza in plant growth and nutrition has been related to uptake of immobile ions of plant nutrients, such as orthophosphate (Li et al. 2006). The AM hyphal network is important in giving plants access to low mobility ions located far from the root surface. Studies using ^{15}N tracer techniques have shown that AM hyphae can transport N

from soil to roots (Johansen et al. 1994; Mader et al. 2000; Tanaka and Yano 2005; Jackson et al. 2008), but high mobility and rapid movement of mineral N to roots through mass flow (Tinker and Nye 2000) has suggested that AM fungi play little role in plant N nutrition. The AM symbiosis was traditionally considered unimportant in plant N nutrition (Liu et al. 2007).

The AM fungi have been reported to proliferate in organic matter and scavenge the mineral N released from soil organic particles (St. John et al. 1983; Hamel 2004). The hyphae of AM fungi can also take up amino acids (Hawkins et al. 2000; Govindarajulu et al. 2005). Based on the observation of hyphae and vesicles of AM fungi in decomposing leaves of *Myrica parvifolia*, *Myrica pubescens*, and *Paepalanthus* sp., Aristizábal et al. (2004) proposed that AM fungi enter decomposing leaves through vascular tissues and efficiently recycle the mineral nutrients released by microbial decomposers. The ability of AM fungi to use dead organic substrates (Talbot et al. 2008) is a matter of debate, but even if this ability is small or nonexistent, these fungi may be important in N cycling through their influence on the free-living soil microbial community (Andrade et al. 1997; Marschner et al. 2001; Hodge 2003a,b; Aneja et al. 2006), which is responsible for most of the N mineralization, particularly in grassland ecosystems (Stanton 1988). Arbuscular mycorrhizal fungi form symbiotic associations with most land plant species (Newsham et al. 1995) and could importantly influence N recycling from litter and soil organic matter. Hodge et al. (2001) reported that *Glomus hoi*, an AM fungus, enhances organic matter decomposition with no effect on plant growth, but their experiment was of short duration (42 days) and restricted to one AM fungus. As plant demand increases with time, we expect that a study of longer duration may reveal better the availability of N to plant from decomposing organic matter. We also hypothesized that different AM fungal species may have different influence on organic matter mineralization.

In this paper, we propose a key role of the AM symbiosis in linking the process of N mineralization to plant N demand in soil, where the AM symbiosis regulates the recycling of plant residue N into living plant biomass and, in the process, changes the soil environment. We used the perennial grass Russian wild rye (*Psathyrostachys juncea* Fisch. Nevski) and three AM fungal species in a controlled condition experiment where extraradical AM hyphae were allowed to access a patch of ^{15}N-labelled organic residues contained in nylon mesh, which we buried in soil. We examined the effect of arbuscular mycorrhizae on residue decomposition, as compared to a non-mycorrhizal control, and the consequences of this effect on plant growth, the soil environment, and microbial community structure after 24 weeks.

Materials and methods

Plants and AM fungal material

Seeds of Russian wild rye (cultivar Swift) were sown in pots containing 500 g of pasteurized soil (80°C for 3 h). The soil had a pH of 6.5, EC of 0.48 mS, and contained 19.7 μg of NH_4–N, 14.1 μg of NO_3–N, 21.3 μg of PO_4–P, and 324.5 μg of K g^{-1} soil after pasteurization. The soil was taken from a cultivated field located at 20 min northwest of Swift Current, Saskatchewan. This loamy sand is preferentially used by our group, as it is light and retains good physical properties during greenhouse experiments. Pots were inoculated with one of three different AM fungal species or with sterilized inoculant. All pots also received 2 ml of a filtrate (Whatman no. 1) of the three AM fungal inoculum mixed together in equal proportion to also provide inoculum-specific microbial population to control systems. Each mycorrhizal treatment received 1 g of root inoculum thoroughly mixed with the soil. The AM fungal species used were *Glomus intraradices* (Schenck & Smith DAOM 181602), *Glomus claroideum* (Schenck & Smith DAOM 235379), and *Glomus clarum* (Nicolson & Smith DAOM 235378). All AM fungal species were multiplied from spores using corn (*Zea mays* L. var. Sunnyvee) grown for 60 days in a greenhouse. At harvest, roots were washed, air dried, chopped, and stored at 4°C until use. Non-inoculated control plants received 1 g of autoclaved inoculum. Plants were maintained at a day/night temperature of 22/18°C with a 16-h photoperiod in a growth cabinet before transplanting to the experimental pots after 21 days.

Experimental design

Four Russian wild rye seedlings colonized by one of the three AM fungal species or non-mycorrhizal were transplanted in pots. A patch of ^{15}N-labelled organic residues was inserted in each pot at the time of transplanting. The organic residue (OR) patch was made of 4 g of ^{15}N-labelled root and shoot of wheat ground and mixed with some pasteurized soil. The organic material contained 22 mg N, 38% of which was ^{15}N. The patch material was sandwiched between two 20-μm nylon mesh walls held onto a polyvinyl chloride ring. Walls were a wire mesh covered by the nylon mesh (Nitex Bolting Cloth; Wildco, Buffalo, NY, USA) on both sides. The patch was placed in the root zone with mesh facing toward the center of the pot. The small patch volume (0.05 l) as compare to pot volume (6 l) meant that the soil volume available to mycorrhizal and non-mycorrhizal plants was practically the same. Pots were filled with the pasteurized loamy sand. Nitrogen (315 mg NH_4SO_4 pot^{-1}) was mixed in the soil at the start of the

experiment, and 15 ml of a modified Long Ashton nutrient solution containing (in mg l^{-1}) 554 KCl, 200 $NaH_2PO_4 \cdot H_2O$, 244 $MgSO_4$, 520 $CaCl_2 \cdot H_2O$, 1.7 $MnSO_4$, 0.25 $CuSO_4 \cdot 5H_2O$, 0.30 $ZnSO_4 \cdot 7H_2O$, 3.0 H_3O_3, 5.0 NaCl, 0.09 $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$, and 32.9 NaFe-EDTA was added at transplantation.

Treatments were replicated five times, and pots were arranged in a randomized complete block design in the greenhouse. Plants were also maintained at day/night temperature of 22/18°C with a photoperiod of 16 h under mixed natural and supplemental light from Lumalux high-pressure sodium lamps (Osram Sylvania, Mississauga) and were watered as needed. Saucers were used, and watering was done parsimoniously to prevent all N loss during the experiment. Plants were grown for a period of 24 weeks between 22 February and 26 July 2007.

Sampling and analysis

At harvest, plant shoots were cut at ground level, and their biomass was determined after drying at 40°C until constant weight. Roots were recovered on a 2-mm sieve and thoroughly washed with tap water to remove adhering soil. Soil and OR patch materials were sieved through 2 mm before subsampling for further analysis. The OR patch material was dried at 40°C and weighed. Roots were cut into 1-cm fragments, weighed fresh, and subsampled. One subsample was dried at 40°C until constant weight for moisture content determination and total root dry mass calculation and for plant tissue N and P analyses. Ground shoot and root tissue digestion (Varley 1966) was completed, and tissue N and P concentrations were measured by the salicylate/nitroprusside (Noel and Hambleton 1976) and the acidic molybdate/ascorbic acid method (Milbury et al. 1970), respectively, on a Technicon AutoAnalyzer II. The second root subsample was used for the determination of AM root colonization using the gridline intersect method (Giovannetti and Mosse 1980). Roots were cleared in boiling 10% KOH solution for 10 min, rinsed with tap water, and stained for 3 min in boiling ink–vinegar solution (Vierheilig et al. 1998).

Shoots and roots of Russian wild rye, bulk soil, and OR patch material were ground to a fine powder in a ball mill. The ground samples were analyzed for ^{15}N content by NCA analyzer Carlo Erba NA1500 coupled to a mass spectrometer Optima. Total C and N in OR patch material was analyzed using Carlo Erba NA1500 NCS analyzer. The amount of N from organic residues remaining in OR patches (N_{ORr}) at harvest were calculated as:

$$N_{ORr} = \left({}^{15}N_{tot} \times N_{tot} - 0.3663 \times N_{tot}\right) / \left({}^{15}N_{ORi} - 0.3663\right)$$

where "N_{tot}" is the amount of N in the OR patch at harvest, "$^{15}N_{tot}$" is the percentage of ^{15}N measured in the OR patch at harvest, "0.3663" is the percentage of ^{15}N in the soil initially placed in the patch, and "$^{15}N_{ORi}$" is the percentage of ^{15}N in the plant residues initially placed in the patch.

The amounts of N mineralized from OR patches were calculated as the difference between N amounts placed in OR at the start of the experiment and N amounts at the end of the experiment (N_{ORr}). The percentage of mineralized N recovered by plants was calculated as:

$$\%\ \text{recovery} = \frac{100({}^{15}N_s \times N_s + {}^{15}N_r \times N_r)}{\text{N mineralized from OR patch}}$$

where $^{15}N_s$ and $^{15}N_r$ are the percentages of ^{15}N measured in shoot and root, and N_s and N_r are the total N content in shoot and root, respectively.

We sought inoculation treatment effects on the structure of the soil microbial community active in the soil with decomposing OR through comparison of their phospholipid fatty acids (PLFA) profiles. PLFA were analyzed as described previously (Hamel et al. 2006). Briefly, soil lipids were extracted from 4 g of soil in dichloromethane/methanol/citrate buffer (1:2:0.8 v/*v*). Lipid-class separation was conducted in silica gel columns. Fatty acid methyl esters from the phospholipid fraction were created through mild acid methanolysis. Fatty acid methyl esters dissolved in hexane were analyzed using a Varian 3900 gas chromatograph equipped with a CP-8400 autosampler and a flame ionization detector. Methyl nonadecanoate (19:0, Sigma Aldrich) added to samples served as an internal standard for the quantification of fatty acid methyl esters (FAME). Helium was the carrier gas (30 ml min^{-1}), and the column was a 50-m Varian Capillary Select FAME # cp7420. Peak identification was based on comparison of retention times to known standards (Bacterial Acid Methyl Esters #47080-U, Supelco, Bellefonte, USA). The PLFAs i-15:0, a-15:0, i-16:0, and i-17:0 were used as biomarkers for Gram-positive bacteria (Sundh et al. 1997), PLFAs 3OH-14:0 for Gram-negative bacteria (Spring et al. 2000), PLFA 18:1ω9t, 17:0, 15:0, 2OH-14:0, and 2OH-16:0 as general bacteria biomarkers (Kawashima et al. 1996; Sundh et al. 1997; Spring et al. 2000), and PLFAs 18:2ω6c and 18:1ω9c for fungi (Petersen and Klug 1994; Sundh et al. 1997). The fatty acid nomenclature follows the omega form, *A*:*B*ω*C*, where *A* designates the number of carbon atoms, *B* the number of double bonds, and *C* the distance of the closest unsaturation from the aliphatic end of the molecule. Prefixes i- and a- refer to iso and anteiso methyl-branching. The suffixes c and t indicate *cis* and *trans* geometric isomers. Hydroxy groups are indicated by OH.

Hyphal length density (HLD) in bulk soil was measured using the line intersect method (Newman 1966). Hyphae

were extracted using a flotation–centrifugation technique (Dalpé and Hamel 2008). Hyphae were stained for 5 min with trypan blue (Koske and Gemma 2000) in the filtration unit. The stain was washed with distilled water and hyphae were counted under a dissecting microscope. Hyphal lengths were calculated using the following formula.

$$HLD = \pi NA/2H$$

Where N is the number of intersects between hyphae and the nitrocellulose filter gridlines, A is the surface area of filter, and H is the total length of lines. Hyphal length densities for each treatment was calculated from hyphal lengths and expressed as mm g^{-1} soil. Background values from uninoculated control were subtracted, and values above control were considered AM hyphal length densities (HLD_{AM}).

Statistical analysis

The significance of treatment effects on soil and plant variables were assessed by analysis of variance using JMP 3.2.6 (SAS Institute, Cary, USA), and means were compared using Fisher's least significant difference test at α=0.05. Differences in soil microbial community composition was determined by discriminant analysis (Huberty 1994) using normalized and standardized PLFA biomarker values using the backward stepwise procedure in Systat v. 12 (Point Richmond, USA). At each step, the biomarker with the least F-to-remove value was removed from the model, until no biomarker with value below 0.15 remained. Regression analysis was conducted using JMP 3.2.6 to relate the level of AM root colonization and mineralized N recovery by plants.

Results

Mycorrhizal development

All three AM fungal species produced AM colonization levels ranging from 18.8% to 25.6% in the roots of Russian wild rye (Table 1), levels similar to those that can be observed in the field in our area. Uninoculated plants showed no colonization at harvest (Table 1). Colonization was highest in *G. clarum*-inoculated plants, while *G. claroideum* colonized Russian wild rye to a lesser extent. Conversely, *G. clarum* had lower HLD_{AM} than *G. claroideum* and *G. intraradices* in rooting soil (Table 1).

Mineralization of organic residue and microbial community in OR patches

The carbon-to-nitrogen ratio in the OR patch material had decreased from an initial level of 17.8 to less than 13 at harvest and was lower in the presence of AM fungi (Table 1), indicating that organic matter decomposition proceeded further in AM than non-mycorrhizal systems. Accordingly, we found larger (P= 0.01) amounts of mineralized N in the presence of AM fungi than in control systems (Table 1).

The structure of the microbial communities colonizing the decomposing patch material under differed inoculation treatments was distinct (Fig. 1). Discriminant analysis classified 100% all microbial communities into their respective inoculation treatment based on their PLFA profiles (Wilk's lambda=0.003, P= 0.004), indicating that inoculation treatments had shaped microbial communities. Only one soil microbial community associated with *G. intraradices* was misclassified as belonging to a *G. clarum*

Table 1 Amount of N mineralized from organic residue over the 24-week growth period, final C-to-N ratio of the OR patch material, Russian wild rye shoot dry weight (DW), root DW, N concentration in shoot and root, arbuscular mycorrhizal (AM) root colonization and AM fungi hyphal length density (HLD) in rooting soil at harvest, as influenced by inoculation treatments

Inoculation treatments	Control	*G. claroideum*	*G. clarum*	*G. intraradices*
N mineralized from residues (mg)	1.41 c	2.91 ab	4.02 a	2.73 b
Patch materials C-to-N ratio	12.3 a	9.8 b	9.6 b	9.8 b
Shoot DW (g)	10.7 b	10.7 b	12.4 a	13.2 a
Root DW (g)	9.9 b	10.2 b	14.4 a	13.3 a
Shoot N (mg g^{-1})	15.9 b	19.0 b	33.5 a	16.2 b
Root N (mg g^{-1})	12.6 a	13.2 a	11.5 a	12.3 a
Shoot P (mg g^{-1})	2.1 a	2.2 a	2.0 a	2.1 a
Root P (mg g^{-1})	1.7 a	1.4 a	1.5 a	1.5 a
AM colonization (%)	0	18.8 b	25.6 a	21.3 ab
AM fungi HLD (mm g^{-1} soil)	0	6.17 a	5.35 b	6.74 a

Means (n=5) followed by different letters in the same column are significantly different at P<0.05 according to Fisher's protected least significant difference test

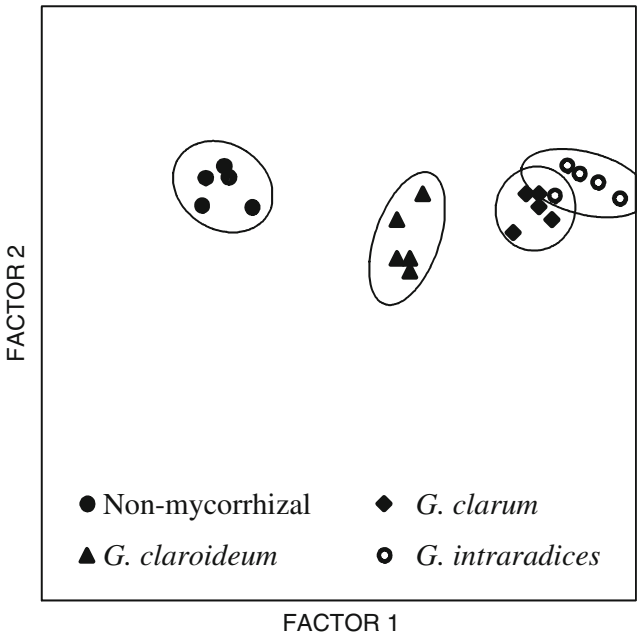

Fig. 1 Biplots from a discriminant analysis showing the effect of inoculation treatments on the microbial community structure in organic residue patches after 24 weeks. Microbial communities in organic residue patches can correctly be classified into their respective inoculation treatments based on PLFA biomarker profile (Wilk's lambda=0.003, P=0.004)

colonized soil. Variation in microbial community structure in OR patches was due to modifications in bacterial and fungal saprotrophic populations. Six bacterial biomarkers (15:0, i-16:0, i-17:0, 17:0, 2OH-14:0, and 2OH-16:0) and three fungal saprotroph biomarkers (18:1ω9c, 18:2ω6c, and 18:1ω9t) were retained as the explicative variables in the model. Inoculation treatments induced qualitative changes in the structure of microbial communities in the OR patch material but did not significantly influence total microbial biomass, as estimated by the sum of microbial PLFA biomarkers in lipid extracts (data not shown).

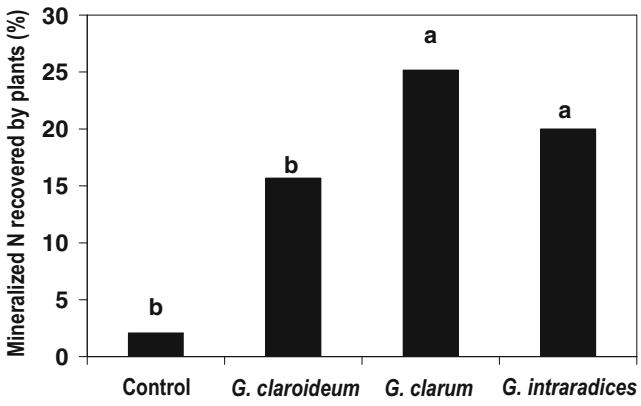

Fig. 2 Proportion of the N released through mineralization of organic residues that was recovered by Russian wild rye plants inoculated or not with different AM fungal species. Means (n=5) followed by different letters in the same column are significantly different at P< 0.05 according to Fisher's protected least significant difference test

Plant biomass and nutrition

Shoot and root dry mass varied with inoculation treatments. Russian wild rye in symbiosis with *G. clarum* and *G. intraradices* produced 16% and 23% more shoot biomass than non-mycorrhizal control plants, while average shoot biomass of *G. claroideum*-colonized plants did not significantly differ from control (Table 1). Root dry mass of *G. clarum*-inoculated plants was 45% and 34% larger than that of control plants (Table 1).

Russian wild rye shoot N concentration was increased by *G. clarum*, but no inoculation effects were found on the concentration of P in shoot (P= 0.56) or root (P= 0.20; Table 1). This indicates that plants were P sufficient, but N limited, a limitation that was relieved by *G. clarum*. Plants colonized by *G. clarum* or *G. intraradices* were the most effective to capture the N mineralized in the OR patch (Fig. 2). A strong relationship (R^2=0.80, P< 0.001, N=20) between mineralized N recovery by plants and AM root colonization level suggests that the extent of root colonization is important in determining N mineralization and transfer by AM fungi to plants.

Discussion

We verified that arbuscular mycorrhizae can increase the mobilization and plant use of N from decomposing organic residues and found that this effect can be important in N cycling. The presence of AM hyphae in OR patches increased N mineralization by 228%, on average. Up to 25% of mineralized N was recovered by AM Russian wild rye plants, after 24 weeks, and this proportion would have probably been larger if mineralized N diffusion from the patch to plant roots was not minimized by the double mesh walls of OR patch containers. Hodge et al. (2001) measured about 15% of patch N recovery in mycorrhizal *Plantago lanceolata* in an experiment that lasted only 42 days. It appears that plants can stimulate the mineralization of OR in soil through C investment in AM fungi development. Observations of enhanced N mineralization and plant recovery of mineralized N reveal a role for AM fungi in the regulation of efficient N cycling in soil, where these fungi link plant N needs to N mineralization. The data show that in the absence of AM hyphae, OR mineralization proceeds slowly, reducing the risk of N loss from the system, since NO_3^- is susceptible to denitrification and leaching

losses. It appears that stimulation or N mineralization by AM hyphae may be regulated by plant N demand, as high soil N availability reduces AM fungi extraradical development (Liu et al. 2000), which has been related to plant uptake of mineralized N (Hodge 2003b; Hodge et al. 2001).

We can attribute plant growth enhancement in *G. clarum* inoculated systems to improved N nutrition. Increased plant tissue N concentration and absence of effect on tissue P concentration clearly indicate that *G. clarum* relieved N deficiency in its host. The cause of improved plant growth with *G. intraradices* is less clear, as the concentration of nutrients in plant tissues were not different from that of control plants. Finally, inoculation with *G. claroideum* did not influence plant biomass production. Although all AM species could enhance N mineralization from the OR patch, this effect was not always associated with improved plant productivity, showing difference in functionality among the AM fungal species.

We found that the extent of extraradical development might not be the only factor involved in AM-induced N mineralization enhancement. *G. clarum* seemingly produced less extraradical hyphae in the bulk soil but enhanced most N mineralization. The fact that the growth of fungus may have been preferentially stimulated in the OR patch cannot be ruled out, however. *G. clarum* enhanced transport of N to plant and plant biomass production despite it having the lowest HLD_{AM} development. Better plant growth performance with *G. clarum* was associated with higher AM root colonization, however, suggesting that a bottleneck at the plant–fungus interface might be a factor limiting effective N transfer from decomposing organic matter to plants via AM fungal hyphae.

The faster decomposition of organic residues in OR patches in the presence of AM fungal hyphae could be due to direct or indirect effects. Direct effects of arbuscular mycorrhizae on organic residue decomposition could be due to enzymatic decomposition by extraradical AM hyphae. The mycelium of AM fungi proliferates in organic residue (Ravnskov et al. 1999) and has the ability to excrete hydrolytic enzymes (Varma 1999). Various hydrolytic enzymes such as cellulose, pectinase, and xyloglucanase have been reported in external mycelium of AM fungi (Garcia Romera et al. 1991; Garcia-Garrido et al. 1992). These enzymes are known to be involved in the degradation of plant material in soil. The AM fungi can arguably be involved directly in the mineralization of organic residues (Talbot et al. 2008), at least to some extent.

Arbuscular mycorrhizae may also stimulate OR decomposition through their effect on soil microorganisms. Soil microbial growth can be stimulated (Secilia and Bagyaraj 1987; Andrade 2004) and the soil microbial community changed (Posta et al. 1994; Marschner and Crowley 1996a,b) in the presence of arbuscular mycorrhizae or AM hyphae (Andrade et al. 1997; Andrade 2004). We found no difference in active soil microbial biomass between treatments at harvest, but it could have been larger in AM-colonized systems initially and declined with narrowing patch material C-to-N ratio as OR mineralization proceeded. Qualitative changes in microbial community structure may also be responsible for faster organic matter decomposition in the presence of arbuscular mycorrhizae. The AM fungi may influence the soil microbial community through different mechanisms, including modification in plant signaling or defense-related biochemical pathways (Lioussanne et al. 2008) and the modification of the nature, amount, and distribution of plant-derived C compounds in soil (Toljander et al. 2007). Extraradical hyphae of AM fungi may bring available C to microorganisms of the hyphosphere, allowing them to mineralize recalcitrant soil organic matter, as described in the model of Schimel and Weintraub (2003). In the absence of AM effect on the abundance of microbial PLFA biomarkers, Hodge et al. (2001) concluded to the probable direct involvement of *G. hoi* in N mineralization from OR. However, a biomass similar in size but more active could have enhanced mineralization in that study. In addition, hyphospheric effects could have been diluted and masked by a large soil volume in the OR compartment used. The observation of better N uptake in a non-host plant species in soil with AM fungi (Hodge 2003a) indicates that, directly or not, these fungi can enhance substantially N cycling in soil.

We observed differences in the structure of soil microbial communities in OR patches after 24 weeks. These differences may reflect both the influence of arbuscular mycorrhizae and that of organic materials at different stages of decomposition under different treatments. Change in the soil microbial community with decomposing organic residue was reported in other studies (Aneja et al. 2006; Ha et al. 2008). Decrease in the abundance of easily metabolized compounds with time drives a microbial succession for decomposing residues. Different carbon-to-nitrogen ratios in the OR patch material under different treatments indicates that OR mineralization had proceeded further in the presence of AM hyphae and, thus, that different qualities of soil organic matter could select soil microbial communities with different structure.

Results suggest new pathways of influence by arbuscular mycorrhizae on plant–soil ecosystems. We have shown that arbuscular mycorrhizae link plant N needs and growth to OR mineralization, modifying the abundance of soil resources and impacting the structure of the soil microbial community.

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